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A QUANTITATIVE DESCRIPTION OF PHOTOSYNTHETIC AREA IN WINTER WHEAT CROPS

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Abstract

A function is introduced to describe the production and senescence of total green area for winter wheat. The equation, fitted by least squares, gave a good representation of observations with both days after sowing and accumulated day degrees used as a time variable. Meaningful growth and senescence quantities can be derived which prove useful in the analysis of foliage increase and decline.

Introduction

Total dry-matter production and crop growth rate, in cereals, are both linearly and positively related to intercepted photosynthetically active radiation (Gallagher and Biscoe, 1978). Crop growth will therefore be determined by the amount of solar radiation available and the crops ability to intercept it. Monteith (1977) reports little variation in incident

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radiation per unit area between neighbouring sites and seasons. This implies that differences in dry-matter accumulation may be attributed to differences in the pattern of foliage production as suggested by Puckridge and Ratkowsky (1971).

It follows that any complete analysis of wheat crop performance must consider canopy production and senescence.

Mathematical functions can be used to describe the pattern of photosynthetic area increase and decline (Clarke and Simpson, 1979; Littleton et al., 1979; Dale et al., 1980; Milford and Riley, 1980; Causton and Venus, 1981). Their use in this context is fourfold:

1. Curves serve to 'smooth out' irregularities resulting from destructive sequential harvest measurements and provide an estimate of inter-harvest trends. The description of growth provided by the function is free from random fluctuations.

2. Parameters in the equation may exhibit biological validity, being related to actual biological mechanisms inherent in the response studied. An examination into the behaviour of these parameters against certain environmental and agronomic variables, may provide a valuable research tool to glean further insight into the particular mechanism they represent.

3. The function may prove useful in models of photosynthetic area production. Doraiswamy et al. (1978) in an extensive review of yield modelling, stressed the frequent requirement of a photosynthetic area sub-model.

4. It may be possible to examine the effects of husbandry treatments independent of season. This has wide applications for the comparison of measurements from different sites or seasons.

A revised form of classical growth analysis using integral values has been described by Ondok and Kvet (1971). Integral comparisons have been used in the study of foliage production (Dormer, 1965; Kvet et al., 1969). Furthermore, the calculation of growth characteristics using the integral approach is reliant upon a measurement of the integrated value of photosynthetic area over the growing season (leaf area duration; Watson, 1952). A function relating canopy area to a time variate may prove useful in this respect.

Methods and Analysis

The Model

Fig. 1 shows the pattern of photosynthetic area (Fischer, 1975) production and senescence. An initial period of gentle positive slope is followed by a more rapid increase reaching a maximum, after which a final senescence phase of negative slope occurs (see also Connor, 1975; Fisher, 1975). A curve exhibiting this pattern can be represented by the equation:

$$l = p\,(m-t)^{q}\,e^{r(t-m)} \qquad (1)$$

If crop lamina or total green area (l) is fitted to a time variate (t) the rate of production of l is proportional to the parameter r, and the rate of senescence of l proportional to q. The constant m, is equal to the maximum value of t when l is zero. Thus the time over which assimilatory opportunity occurs lies between t = 0 and t = m. p, is a constant which scales the curve on the l axis. The relation of these parameters to aspects of canopy production introduces an element of biological validity (Wiley and Heath, 1976; Landsberg, 1977) to an otherwise empirical approach

although Hunt (1979) suggests that this is not a prerequisite for curve fitting. Where parameters of a model have an intelligible biological or physical meaning the function is termed 'realistic' (Sprent, 1967).

Equation (1) may be viewed as a two stage interactive process of exponential increase, $e^{r(t-m)}$ as suggested by Ondok (1971), and power law decline, $(m-t)^q$.

Differentiating l with respect to t:

$$dl/dt = p(m-t)^{q-1}\ e^{-r(m-t)} \left\{(m-t)r-q\right\} \qquad (2)$$

which = 0 when $t \to -\infty$ and $t = m$.

This shows the maximum photosynthetic area (l_{max}) to lie when:

$$t = m - q/r = t_m \qquad (3)$$

and the value of l_{max} is:

$$l_{max} = p(q/v)^q e^{-q} \qquad (4)$$

From further differentiation the maximum rate of leaf area production (u) lies at a time (t_u) given by:

$$t_u = m - \left(\frac{q + \sqrt{q}}{r}\right) \qquad (5)$$

and the minimum rate of leaf area production, maximum rate of senescence (w) lies at a time (t_w) given by:

$$t_w = m - \frac{q}{r} + \sqrt{\frac{q}{r}} \qquad (6)$$

By substituting t_u or t_w for t in equation (2) u and w are found accordingly:

$$u = p\sqrt{q}\left(\frac{q+\sqrt{q}}{r}\right)^{q-1} e^{-(q+\sqrt{q})} \qquad (7)$$

$$w = -p\sqrt{q}\left(\frac{q-\sqrt{q}}{r}\right)^{q-1} e^{-(q-\sqrt{q})} \qquad (8)$$

A mean rate of canopy production (b) can be found by:

$$b = l_{max}/t_m \qquad (9)$$

and a mean senescence rate (c) is given by:

$$c = l_{max}/(t_m - m) \qquad (10)$$

If we put $z = r(m-t)$:

$$l = \frac{p}{r} z^q e^{-z} \qquad (11)$$

and

$$\int l \, d_z = \frac{p}{r} \int z^q \, e^{-z} \, d_z \qquad (12)$$

is a gamma function whose properties are well known (e.g. Spiegel, 1963). In the special case of q being an integer, this reduces to a factorial.

In any optimisation procedure maximum accuracy is obtained if the parameters are of the same order (NAG, 1982). Arbitrary scaling factors were included for the iteration procedure and it was necessary to introduce a further scaling factor of 1000, resulting in the following transformation:

$$l = p \, (M-t/1000)^{Q} e^{-R(M-t/1000)} \qquad (13)$$

Equation (11) was fitted to bivariate observations of l upon t by least squares using the method suggested by Gill and Murray (1978).

Leaf senescence has been shown to follow a linear decline with time (Littleton et al., 1979). An estimate of M can thus be found using a linear regression on observations of l decline during the senescent phase.

Leaf lamina, sheath and peduncle area were measured using an electronic planimeter, ear area being determined arithmetically by the method of Gallagher and Biscoe (1978).

Measurements were available for three seasons from crops grown on the University of Nottingham Farm at Sutton Bonington.

During 1973-4 and 1976-7 seasons, crops of winter wheat (cv. Huntsman) grown following 'normal farm practice' were monitored. Each bivariate observation, used in the curve fitting exercise, was a mean of six replicate measurements. Site details have been given by Gregory et al. (1978) and husbandry details given by Gallagher and Biscoe (1978).

Finally, a field trial, 1980-81 season, allowed the effect of nitrogen fertilizer (ammonium nitrate) application on LAI and GAI to be examined. A single early (leaf appearance stage 4 + 1) dose was applied at five rates; 0, 50, 100, 150 and 200 kgN ha^{-1}. The design was randomised block with all other husbandry factors assuming standard practice (MAFF, 1976). Soil analysis revealed a very low residual nitrogen content as the trial followed three previous cereal crops.

Two indices of time were tried in the analysis. Calendar time was used in the form of accumulated number of days after sowing (D.A.S.).

Temperature affects plant development through its influence on the rate of metabolic processes (Hodges and Doraiswamy, 1979). Nuttonson (1953) showed that temperature is a major determinant of cereal development in the field. Later Williams and Biddiscombe (1965) demonstrated the rate of grass leaf extension to be closely correlated with temperature, a relation which proved consistent for wheat (Gallagher, 1979a; Gallagher, 1979b; Kemp, 1980). An arbitary scaling measure used to describe the influence of temperature on plant development is growing degree days (Hodges and Doraiswamy, 1979) or thermal time (Gallagher, 1979a). The use of thermal time in describing crop relationships is extensive (e.g. Nuttonson, 1948; Robertson, 1968; Hodges and Doraiswamy, 1979; Squire, 1979).

Thermal time was calculated assuming daily temperature follows a sine wave course between maximum and minimum recorded temperature. The integral

of the curve above a base temperature of 0°C (Biscoe, 1979; Gallagher, 1979a) gives the appropriate thermal time for that day. This index was tried as an alternative time variate in the curve fitting procedure described above.

Results and Discussion

Equation (13) was fitted to the data assuming normal distribution of errors with a constant variance. The function provided a close representation of all sets of observations (Figs. 1, 3; Table I).

Time variates

Replacing D.A.S. with thermal time reduced displacement between the two seasons in time causing convergence of growth curves (Fig.1b). Maximum canopy area (l_{max}) occurred (t_m) at an almost simultaneous point in thermal time, but at very different calendar times (see Appendix).

Wheat leaf initiation, appearance and extension rates are linearly related to accumulated temperature (Gallagher, 1979a). Dates of individual leaf extension are also directly related to crop leaf area expansion (Gallagher, 1979b). The duration of leaf expansion is further related to temperature (Gallagher, 1979a). Visible reduction in seasonal variation between seasons using thermal time, may be attributed to removal of the influence of seasonal temperature differences. Remaining variation between crops seen in Fig. 1b. is due to husbandry factors, edaphic factors and remaining climatic factors such as daylength (Baker et al., 1980) and light intensity (Walpole and Morgan, 1971).

Fig. 2 shows the shape of the differential curve for the 1976-7 season. The curve indicates how rates of leaf growth and senescence, from equation (2) change during the crop growth.

Analysis of the effects of fertilizer nitrogen on photosynthetic area

We now examine the use of equation (1) in analysing the effects of agronomic treatments, in this case nitrogen fertilizer on photosynthetic area. A close fit was achieved in each case (Fig.3; Table I). Fig. 3 gives a diagramatic representation of increased canopy size following the application of successive increments of ammonium nitrate. Growth attributes were calculated (given in the Appendix) and used to analyse the specific effects of nitrogen on canopy production. Increases in the maximum (u;equation, 7) and mean (b;equation 10) rates of canopy growth led to an increase in maximum size achieved (l_{max}; equation 4). This effect is shown in Fig. 4. The length of the growing season (m) is lengthened by applying nitrogen fertilizer. But this effect is modest and only continues up to 100 kgN ha^{-1} (Table I). It follows that the decline in l, over time m, from higher values of l_{max}, will necessitate faster rates of senescence. This is the case as mean (c;equation 10) and maximum (w;equation 8) senescence rates are faster with increased nitrogen availability (Fig.4).

As wheat growth is directly related to the quantity of radiation intercepted (Gallagher and Biscoe, 1978) it is of interest to show the effects of nitrogen fertilizer on light absorption. The fraction of incident photosynthetically active radiation intercepted, F_p, by l can be estimated from the Monteith formula given by Gallagher and Biscoe (1978).

$$F_p = (1 - \exp(-0.9.k.l))/1.11 \qquad (14)$$

where k, the extinction coefficient is equal to 0.44 for temperate cereals (Monteith, 1975). Fig. 5 shows the pattern of F_p for increasing levels of nitrogen fertilizer. l for equation (14) is estimated from equation (13). This approach may be of use in growth and yield modelling (M.N. Hough, Meteorological Office, personal communication).

Testing using published records

Fitting of equation (13) has so far been applied to crops grown at Sutton Bonington only. It was decided to test the function on sets of published data. There is a dearth of such information in the literature, however, three sets were available: one from wheat grown in Japan (Takeda, 1979) and two from Rothamsted Experimental Station (Lester, 1981; 1982).

Fig. 6 shows the fitted curves, values of parameters are given in Table 1 and derived growth attributes are shown in the Appendix. The advantages of a high frequency of observations in the Sutton Bonington results were not present here. Equation (13) still gave a close representation of photosynthetic area.

Relationships between growth attributes

There is a linear relationship between the mean and maximum rates of canopy production (r^2 = 0.74) and a stronger correlation between similar measures of senescence (r^2 = 0.98, Fig.7). This is probably due to the influence of maximum on mean rates. Variations in the relation between maximum and mean production rate are influenced by the variable length of t_m. As a component of t_m, the initial stage of low growth rate is the most important influence on mean growth rate. The length of this inital stage is determined by sowing date and season, especially temperature during winter months.

Using linear regression technique, it was decided to examine the importance of duration (t_m) and rate (b) of canopy expansion on l_{max} (Fig.8). l_{max} is correlated with both t_m (r^2 = 0.88) and b (r^2 = 0.99) which seems to exert a greater influence.

Conclusion

The function described in equation (1) fitted to scaled time variates (equation 13) gives an accurate representation of photosynthetic area increase and senescence in wheat crops. Using this 'functional' approach (Causton and Venus, 1981; Hunt, 1982) the course of foliage production and decline can be divided into nine quantities:

1. Length of the canopy growing season, m, equation (1)
2. Mean rate of canopy production, b, equation (9)
3. Maximum rate of canopy production, u, equation (7) and
4. its time of occurrence, t_u, equation (5)
5. Maximum size of canopy achieved, l_{max}, equation (4) at
6. a time, t_m, equation (3).
7. Mean senescence rate, c, equation (10).
8. Maximum senescence rate, w, equation (8) and
9. its time of occurrence, t_w, equation (6).

Furthermore an estimate of the course of photosynthetic area can be achieved with limited numbers of bivariate observations. The function, as outlined above, presents a new technique for describing and analysing the effects of seasonal or husbandry factors on the crop canopy.

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TABLE I

Parameters and goodness of fit for photosynthetic area of wheat crops fitted on time variates using equation (10).

	Location	Season	Time Variate	Treatment	$Px10^3$	M	Q	R	R.S.D.
1.	Sutton Bonington	1973-74	Days after sowing	-	1273.13	0.262	3.17	62.07	0.15
2.	Sutton Bonington	1973-74	Thermal time	-	0.77	2.434	4.25	5.26	0.15
3.	Sutton Bonington	1976-77	Days after sowing	-	7.92	0.279	1.67	52.85	0.27
4.	Sutton Bonington	1976-77	Thermal time	-	0.25	2.078	2.28	4.82	0.35
5.	Sutton Bonington	1980-81	Days after sowing	0kgN ha^{-1}	4.95	0.306	1.99	28.51	0.33
6.	Sutton Bonington	1980-81	Days after sowing	50kgN ha^{-1}	78.55	0.319	2.76	35.02	0.34
7.	Sutton Bonington	1980-81	Days after sowing	100kgN ha^{-1}	63.97	0.320	2.63	34.30	0.10
8.	Sutton Bonington	1980-81	Days after sowing	150kgN ha^{-1}	11.84	0.320	2.07	29.79	0.52
9.	Sutton Bonington	1980-81	Days after sowing	200kgN ha^{-1}	59.94	0.320	2.54	34.26	0.38
10.	Japan (Takeda,1979)	1969-70	Days after germination	-	378.17	0.215	2.84	59.04	0.31
11.	Rothamsted (Lester,1981)	1979-80	Days after sowing	-	42.48	0.342	2.35	33.06	0.50
12.	Rothamsted (Lester,1982)	1980-81	Days after sowing	-	31.90	0.349	2.17	33.91	0.32

APPENDIX

Growth attributes for photosynthetic area of wheat derived from parameters in equation (11). See Table I for details of location, season and time variate.

Crop	Treatment	Maximum Area		Maximum Production		Maximum Senescence		Mean Rates	
		l_{max}	t_m	u	t_u	w	t_w	b	c
1.	-	4.29	211	66.4	182	-146.5	240	0.020	-0.084
2.*	-	4.41	1588	5.2	1234	- 10.3	2017	0.003	-0.005
3.	-	4.65	247	76.7	224	-256.1	272	0.019	-0.145
4.*	-	4.64	1605	6.5	1292	- 16.7	1918	0.003	-0.004
5.	0kgN ha^{-1}	3.38	236	27.9	187	- 79.4	286	0.014	-0.048
6.	50kgN ha^{-1}	4.48	240	41.0	193	- 98.8	288	0.019	-0.057
7.	100kgN ha^{-1}	5.38	243	48.9	196	-120.6	291	0.022	-0.070
8.	150kgN ha^{-1}	5.99	250	51.7	203	-146.7	299	0.024	-0.086
9.	200kgN ha^{-1}	6.38	246	58.7	199	-148.9	292	0.026	-0.086
10.	-	4.04	167	62.6	138	-143.8	196	0.024	-0.084
11.	-	8.12	271	76.6	225	-195.1	317	0.030	-0.115
12.	-	9.35	285	89.8	242	-214.7	328	0.033	-0.146

*Using accumulated temperature as a time variate

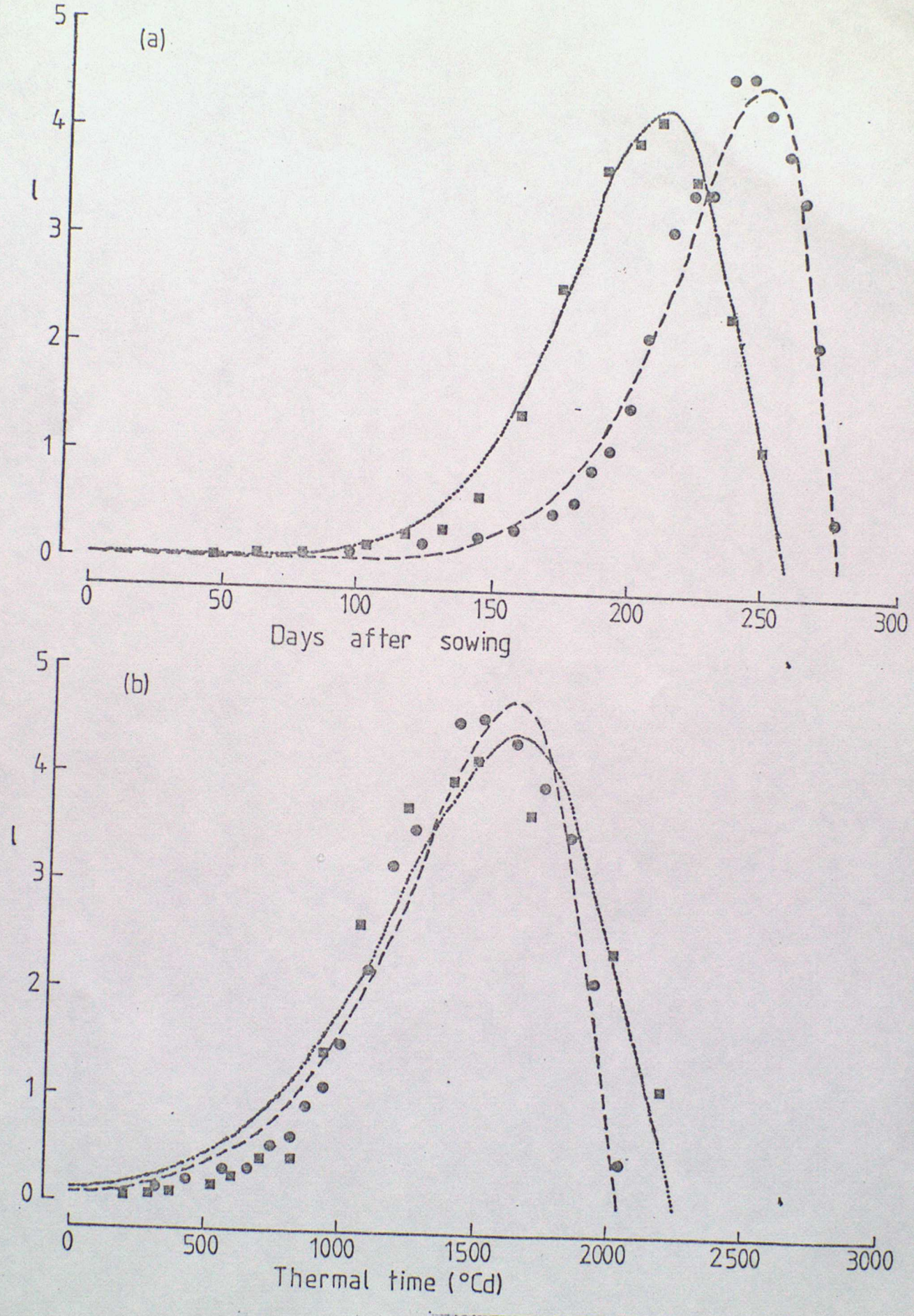


Fig.1. Photosynthetic area in two wheat crops grown at Sutton Bonington 1973-74 (■·····) and 1976-77 (●– – – –) fitted to (a) days after sowing and (b) thermal time.

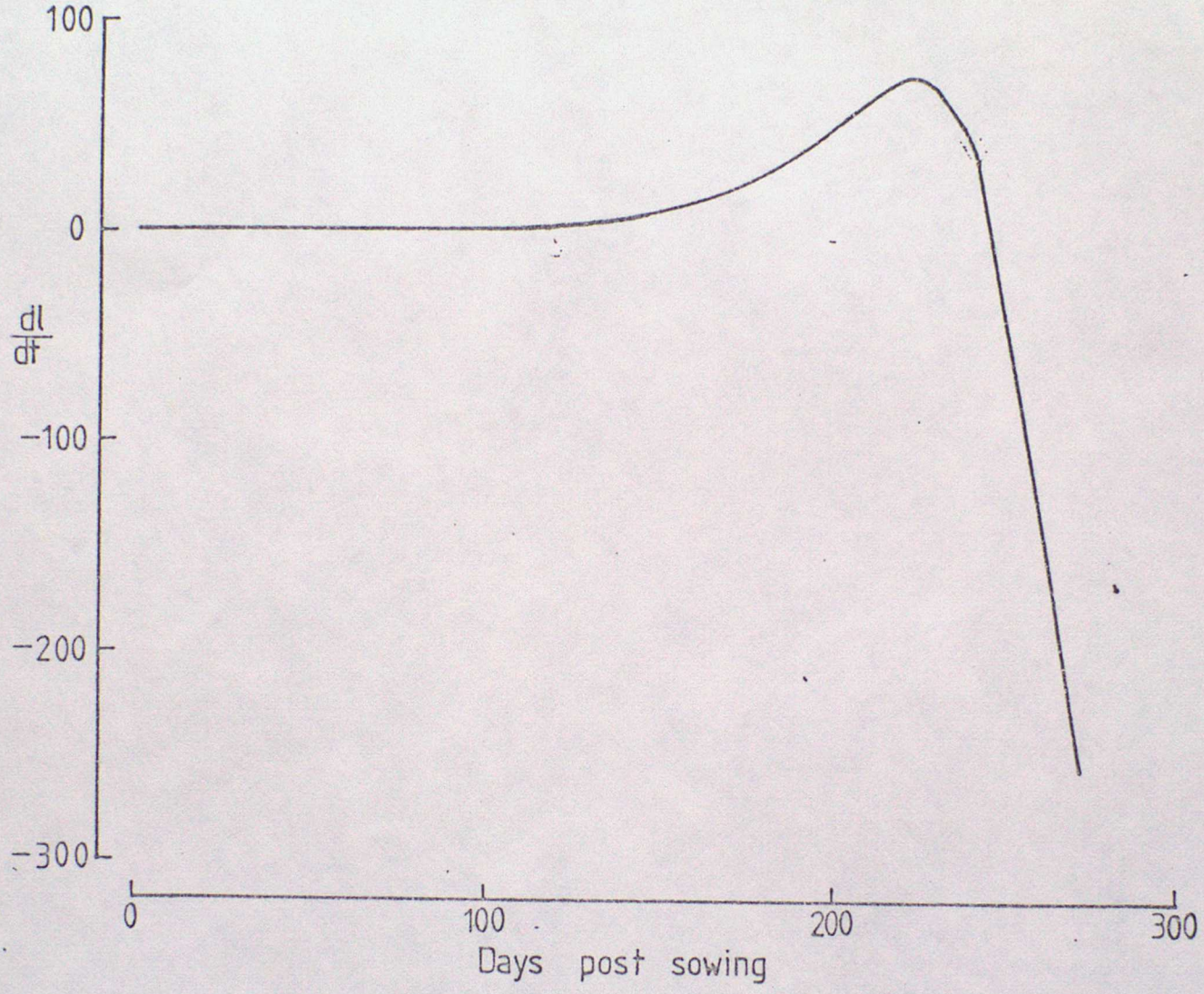


Fig.2. Shape of differential curve (equation 2) relating the rate of canopy production and senescence to time. Data for Sutton Bonington, 1976-77.

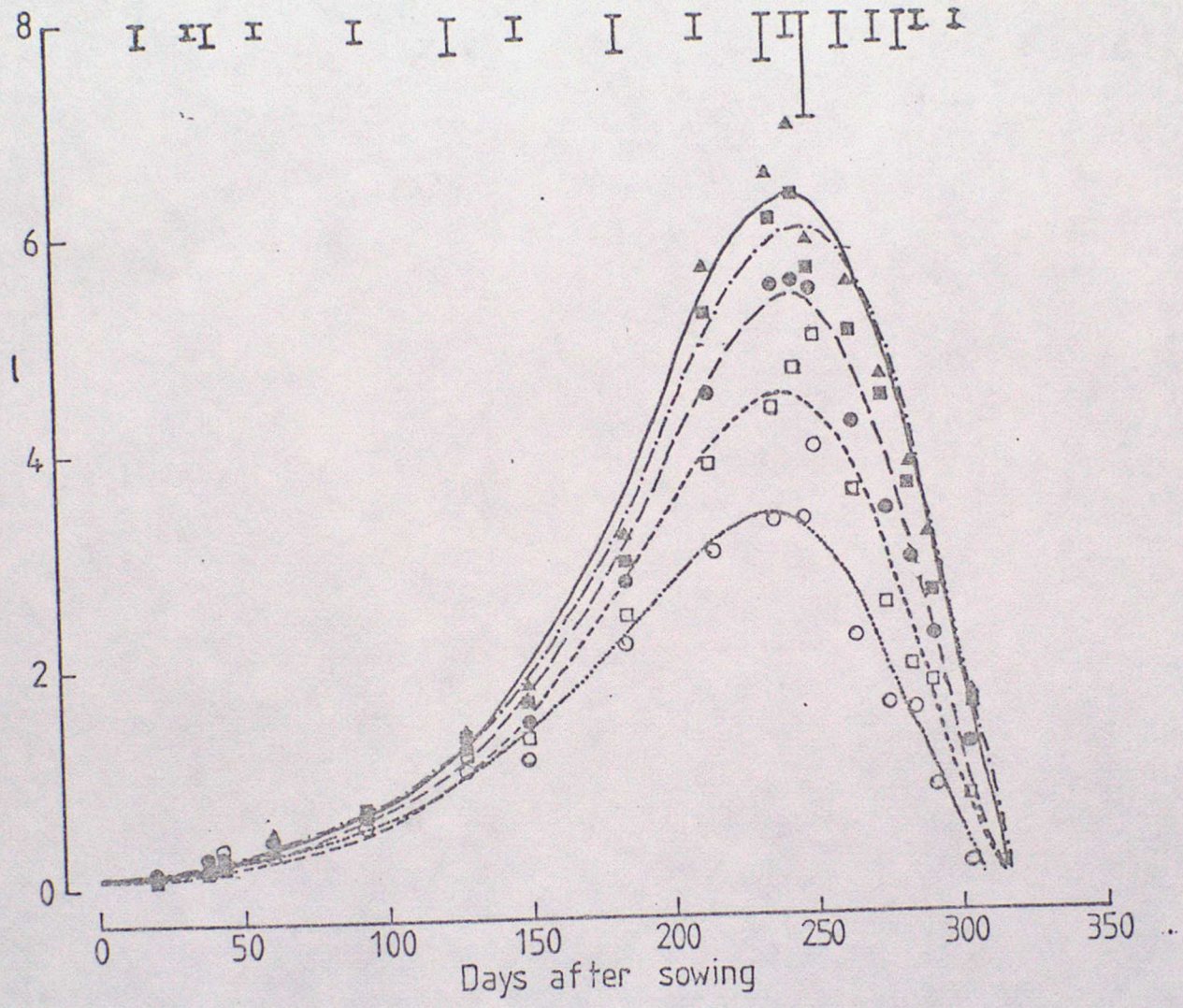
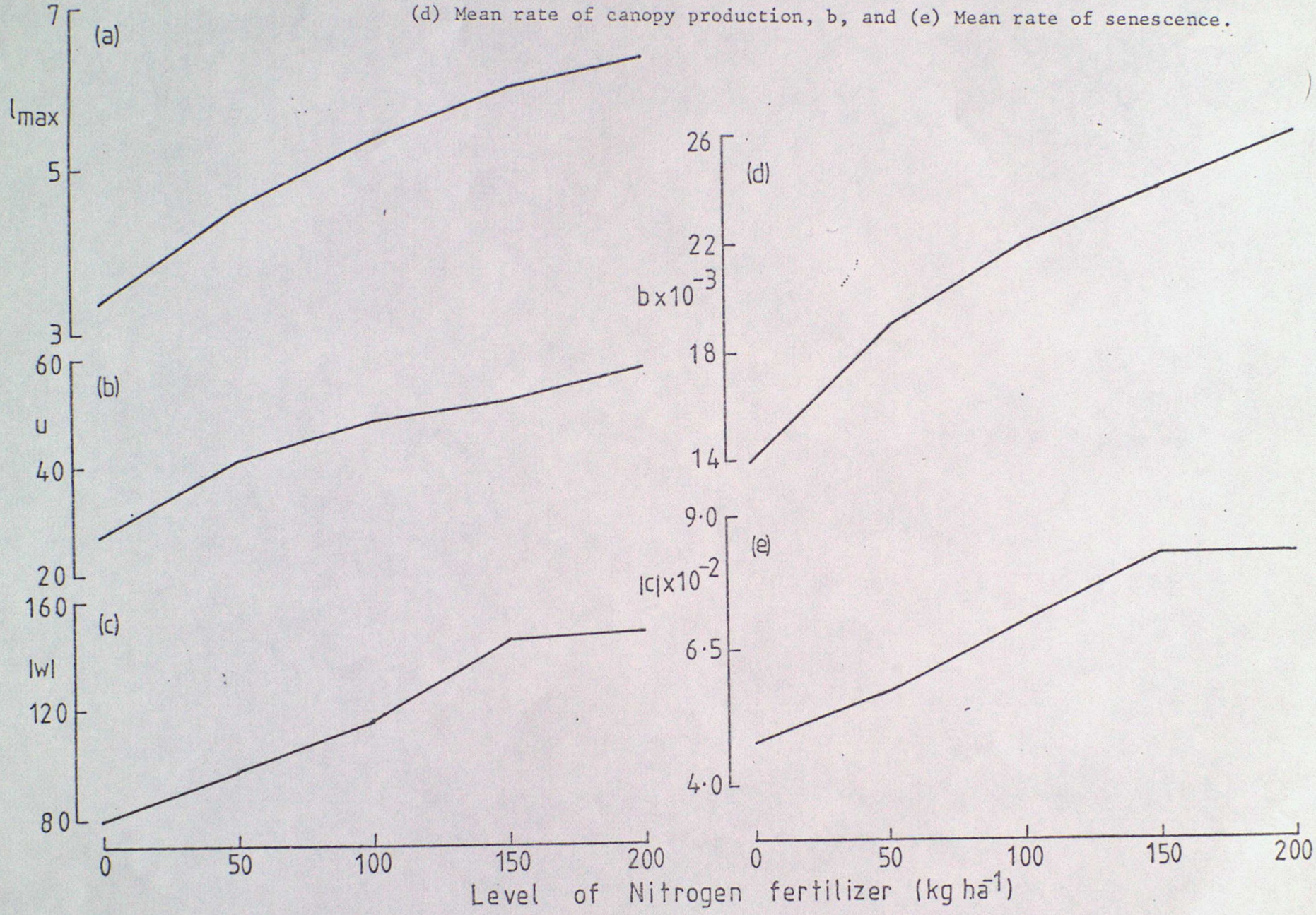


Fig.3. The effect of applied nitrogen on photosynthetic area of winter wheat. Nitrogen rates (O·····) 0kgN ha^{-1}; (□----) 50kgN ha^{-1}; (●——) 100kgN ha^{-1}; (■—·—) 150kgN ha^{-1} and (▲——) 200 kgN ha^{-1}. Vertical bars represent S.E.D.

Fig.4. Behaviour of derived growth attributes as influenced by the application of nitrogen fertilizer. (a) Maximum canopy area achieved, l_{max}; (b) Maximum rate of canopy production, u; (c) Maximum rate of senescence, w; (d) Mean rate of canopy production, b, and (e) Mean rate of senescence.



Frg. 4
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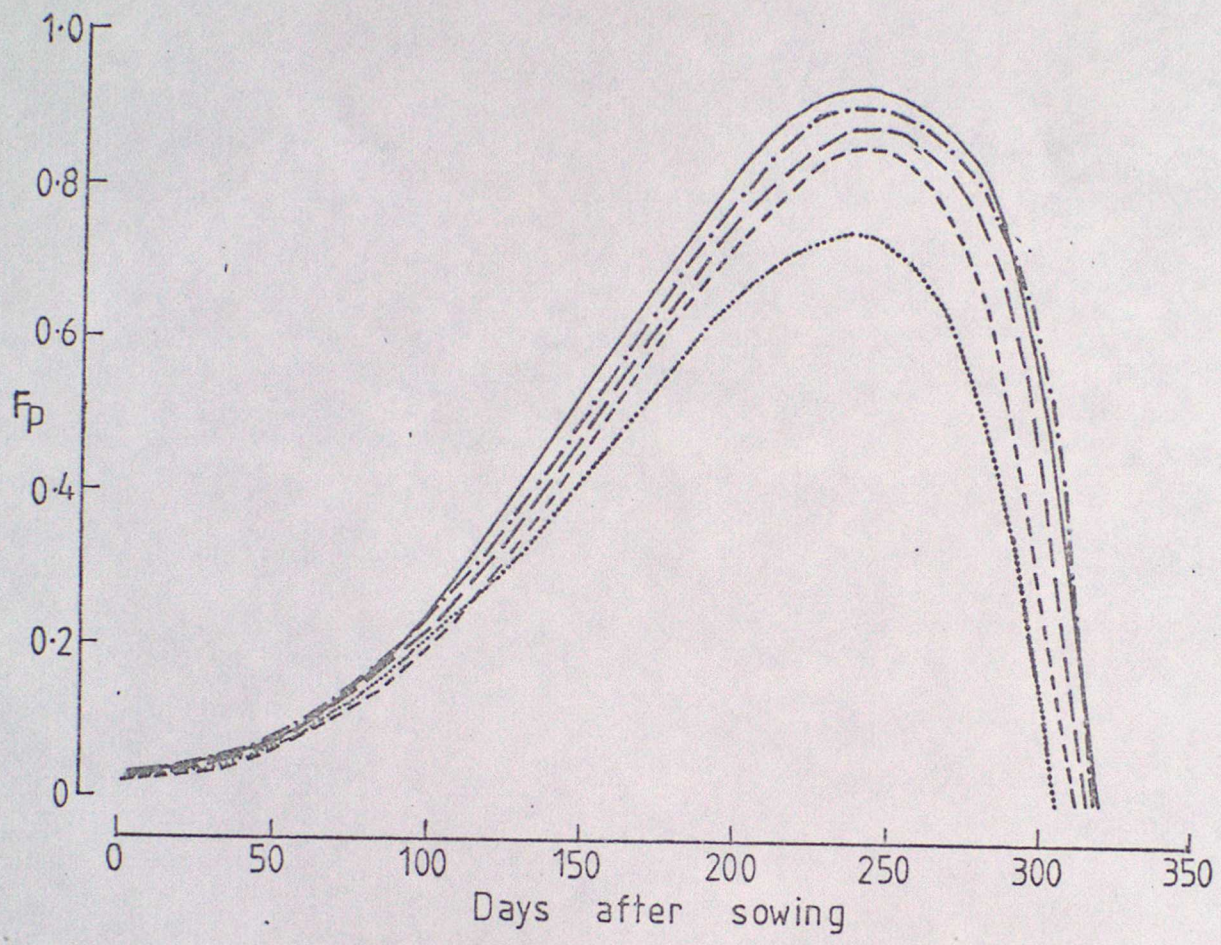

Fig.5. Theoretical proportion of PAR intercepted by canopy (F_p) calculated using values of l estimated from equation (14). Nitrogen rates (·····) 0kgN ha^{-1}; (- - - -) 50kgN ha^{-1}; (— —) 100kgN ha^{-1}; (—·—·) 150 kgN ha^{-1} and (——) 200 kgN ha^{-1}.

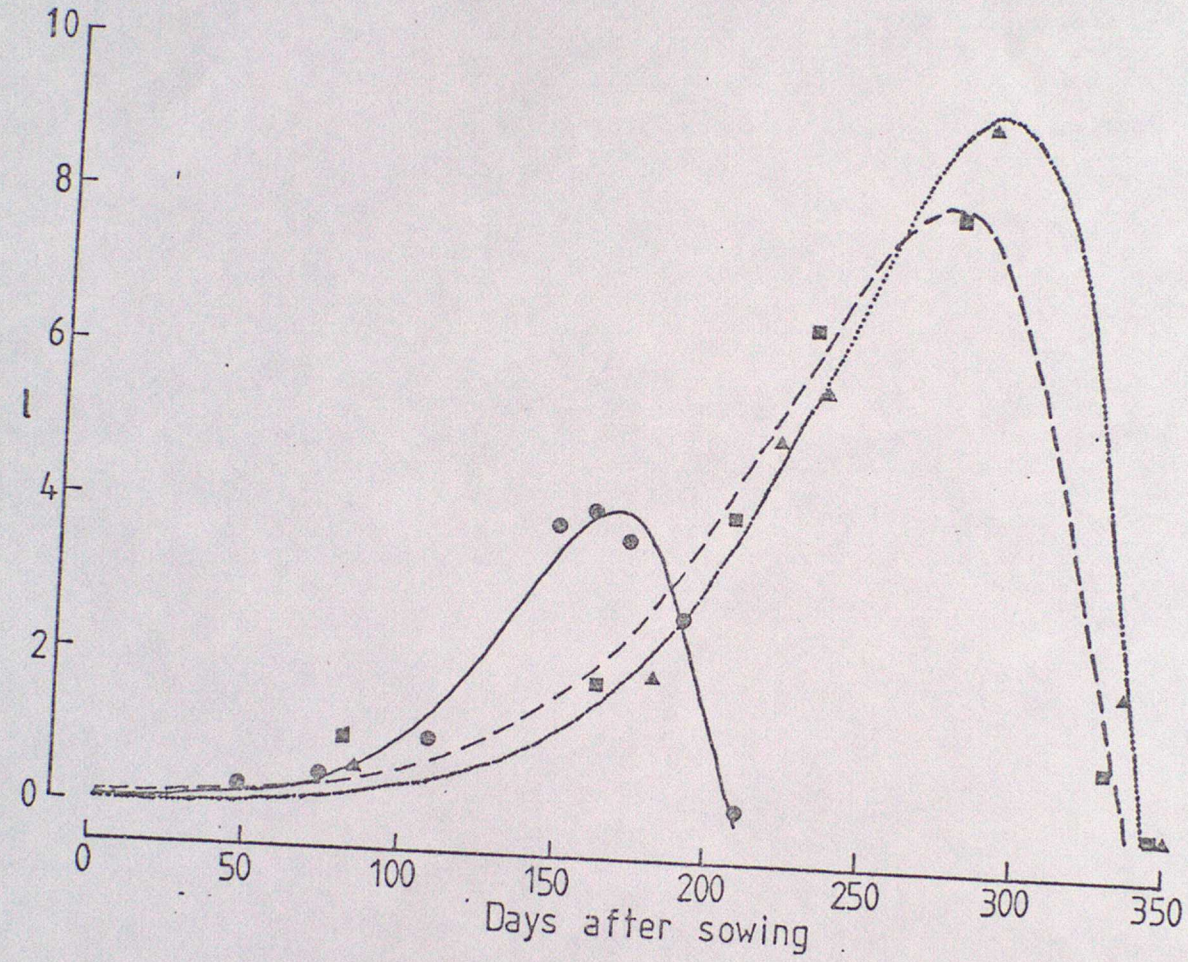

Fig.6. Published values of photosynthetic area fitted to days after sowing. (●——) Takeda, 1979; (■– –) Lester, 1981; (▲·····) Lester, 1982.

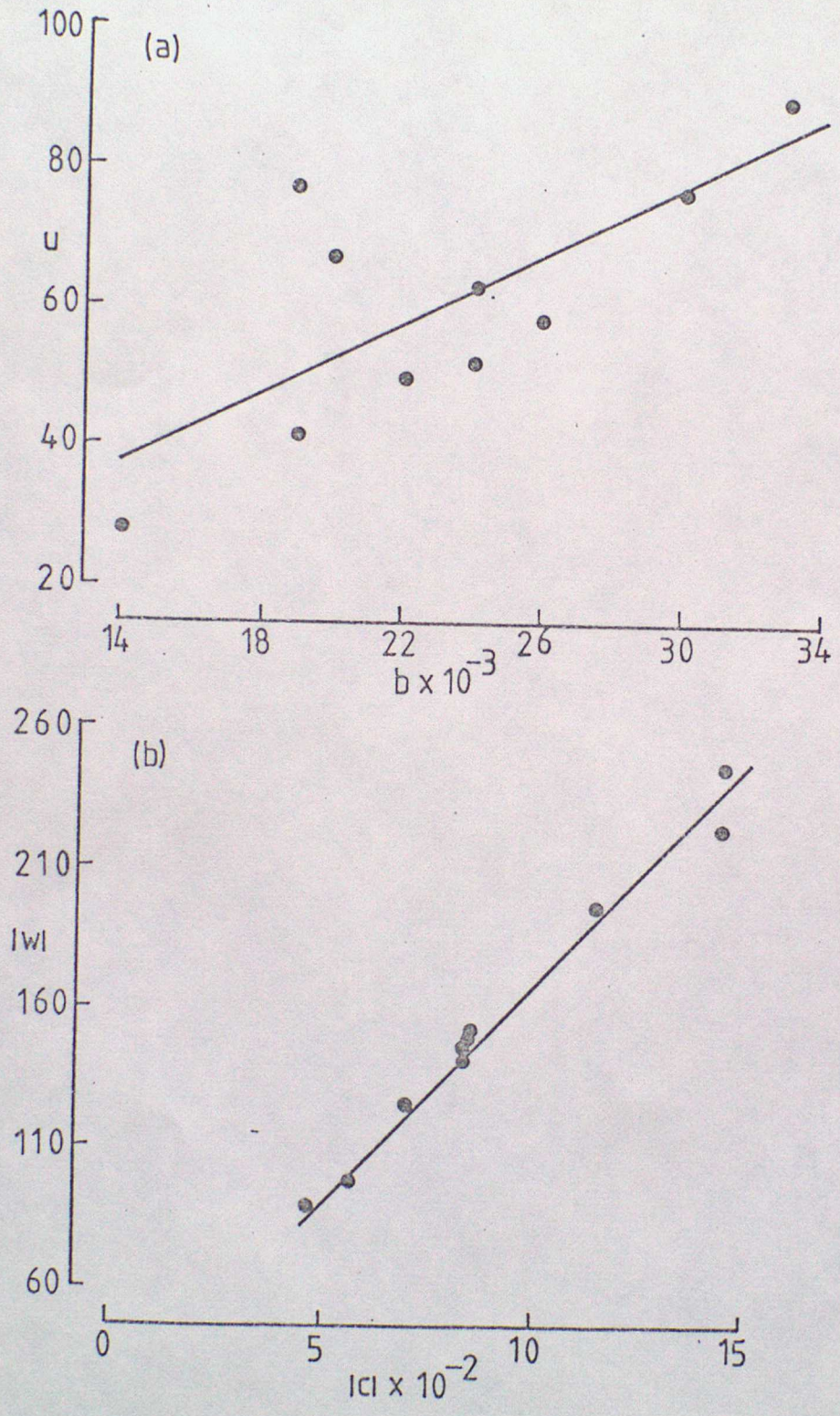

Fig.7. Relationship between (a) the maximum, u, and mean, b, rates of canopy production ($u = 3.32 + 2455.2b$, $r^2 = 0.74$) and (b) the maximum, w, and mean, c, rates of senescence ($|w| = 10.72 + 1565.5\ |c|$, $r^2 = 0.98$).

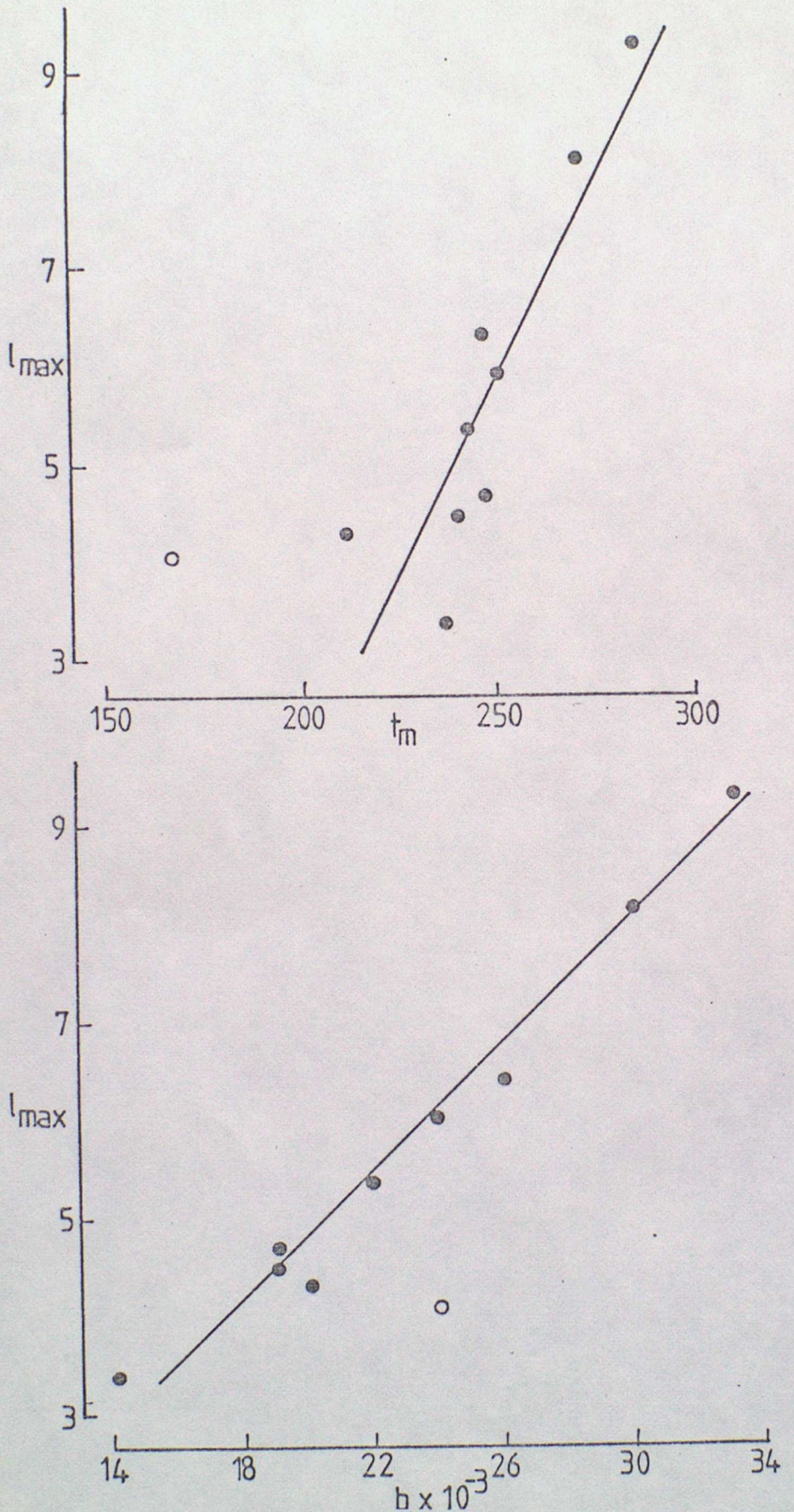

Fig.8. Dependence of maximum canopy size achieved, l_{max}, on (a) the duration of expansion ($l_{max} = -14.2 + 0.081\ t_m$, $r^2 = 0.88$) and (b) the mean rate of expansion, b ($l_{max} = -1.58 + 320.14b$, $r^2 = 0.99$). Regressions omit data from Japan (o).